

TITLE

Bioregionalization approaches for conservation: methods, biases, and their implications for Australian biodiversity

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ACKNOWLEDGMENTS

This study was supported by Australian Research Council Laureate Fellowship (grant number FL160100101).

Abstract

Biogeographic classification schemes have been developed to prioritize biodiversity conservation efforts at large scales, but their efficacy remains understudied. Here we develop a systematic map of the literature on bioregional planning, based on a case study of the Interim Biogeographic Regionalization for Australia (IBRA), to identify where and how such schemes have been used in scientific research. We identified 67 relevant studies, finding that the majority investigated biodiversity exclusively within a single bioregion (65.7%), with 18 of these studies splitting the targeted bioregion based on administrative boundaries. Most used inferential techniques (74.6%) or pattern-based measures (68.7%), and few studies (9%) both considered biodiversity across multiple bioregions and compared findings between bioregions. Species were investigated ten times more frequently than ecosystems attributes, with mammals and birds monopolizing scientists' attention. These findings show that our knowledge of biodiversity at bioregional scales is patchy, even for well-studied taxa, and that we have a limited understanding of the synthetic relationship between biodiversity and IBRA bioregions (which are demarcated according to other biophysical factors). This creates a barrier for systematic conservation planning, which requires unbiased information on the spatial attributes of biodiversity, and therefore this knowledge deficit warrants more attention.

Keywords: Bioregionalization; Terrestrial biodiversity; Australia; Interim Biogeographic Regionalization for Australia (IBRA); Systematic map

Introduction

Biogeographically-based conservation schemes have played an important role in guiding conservation efforts at large spatial scales (Jepson and Whittaker 2002; Whittaker et al. 2005). They have been used to identify areas where biodiversity (e.g., endemic species or habitat) are highly threatened (Hoekstra et al. 2005; Mittermeier et al. 2004), evaluate conservation priorities (Long et al. 1996; Olson and Dinerstein 1998), attract conservation investment to specific regions (Sloan et al. 2014) and to guide environmental policy and biodiversity research (Smith et al. 2018). Yet, biodiversity continues to decline, even in regions prioritized as having high conservation value (Butchart et al. 2010; Rodrigues et al. 2014).

Despite constituting important planning tools, conservation schemes based on biogeographic principles have been criticized on conceptual, methodological and implementation grounds. Although these schemes have incorporated systematic conservation principles (i.e., vulnerability and irreplaceability) to various degrees (Brooks et al. 2006), they typically fail to incorporate complementarity, to optimize the representation of all mapped taxa (Humphries 2001; Mace et al. 2000). Setting priorities using major habitat boundaries or species of one taxon (even if speciose, like birds) may fail to capture diversity in other taxa and biodiversity levels (Brummitt and Lughadha 2003). Using species and endemism as the levels of specificity for analyses can be problematic, because of the possible variance in patterns of richness at different taxonomic levels and the not necessarily positive relationship between species richness and endemism (Whittaker et al. 2005). It has been shown that the unequal size of these schemes' planning units has skewed prioritization results towards planning units of small size, because there was no correction for the nonlinearity of the species-area relationship (Ovadia 2003). Further, the large size of these schemes' planning units has been argued to be impractical for implementation of conservation actions because of the need to move back-and-forth between planning scales before these schemes can be effectively executed on ground (Humphries 2001; Mace et al. 2000). Despite this criticism, which prompted the response

of some of the original biogeographic conservation advocates (Brooks et al. 2006; Myers and Mittermeier 2003), research on how the patterns and processes of biodiversity relates to the spatial units of biogeographically based conservation schemes remains an understudied topic.

Globally, there are marked biases on where, what and how biodiversity is researched (e.g., Clark and May 2002; Fardila et al. 2017; Martín-López et al. 2009). The study of single species has, to date, been the main research focus in scientific fields related to biodiversity conservation (Carmel et al. 2013; Fazey et al. 2005). Research on mammal and bird species is still the dominant trend across biological sub-disciplines (Hecnar 2009; Velasco et al. 2015), with data skewed toward the Palearctic and Nearctic biogeographic realms and focused on developed countries in those regions (Collen et al. 2008; Ondei et al. 2018). Observational and experimental research is most common in ecological research, with an increase in problem-solving studies and the use of secondary sources of data for modeling and big data analysis over the last three decades (Carmel et al. 2013), often at the expense of field-based research (Ríos-Saldaña et al. 2018). Evidence syntheses of the literature on conservation science have also found disparities in the relative effort given to different methodological, geographic or biodiversity foci (e.g., Fardila et al. 2017; Roe et al. 2014). The inconsistency in biodiversity research is systemic; therefore, it is reasonable to expect that biodiversity research based on the spatial units of biogeographic conservation schemes will reflect similar patterns.

Systematic reviews and syntheses are important for evaluating strength of evidence in conservation biology and environmental science (James et al. 2016; Pullin and Knight 2009). Although the gold standard of evidence synthesis is to produce an aggregate quantitative measure of an intervention's impact on a study system (e.g., systematic review, meta-analysis), this is not always feasible, due to the lack of suitable empirical data or the scope of the question of interest (Collaboration for Environmental Evidence 2018). 'Systematic mapping', developed as a response to

this limitation, seeks to describe the nature of a research field in terms of distribution and abundance of available evidence, but also as a means to identify sub-sets of studies suitable for systematic review in one or more areas of the systematic map (Gough et al. 2012; James et al. 2016). In this study, our overall objective was to create a systematic map that charts the factors underpinning our understanding of biodiversity research within the context of bioregionalized conservation schemes. To do this, we considered how bioregions have been studied for conservation, what dimensions of biodiversity have been investigated, and how research effort has been distributed within and across the spatial units of a biogeographically based conservation framework.

To meet these objectives, we chose to focus on the development of research on patterns and processes of Australia's terrestrial biodiversity, based on the spatial units (i.e. bioregions) of the Interim Biogeographic Regionalization for Australia (IBRA) framework. This provides an ideal case study, because Australia is the only megadiverse country (Mittermeier et al. 1997) where a biogeographical approach has been used explicitly to prioritize conservation actions on the ground. Implementation of the IBRA framework has been instrumental in curbing the inherent bias of Australia's national reserve system towards areas of low agricultural productivity (Barr et al. 2016). Nevertheless, conservation of large intact landscapes in Australia has decreased (Watson et al. 2009), and it is recognized that IBRA bioregions and threatened species with relatively large ranges are not uniformly represented (Taylor 2017; Taylor et al. 2014) or adequately protected (Watson et al. 2011). The mixed success of the IBRA framework at conserving biodiversity has, like its global counterparts, been attributed to an inadequate use of systematic conservation planning principles (Craigie et al. 2015) and inherent methodological limitations, though this has yet to be quantitatively assessed.

Methods

Search, selection, classification and summary of the literature

To identify the relevant literature, we searched three databases: Web of Science, Scopus, and Google Scholar. In the first two, the following keyword string was used ([*region* OR biogeograph* OR "IBRA"] AND ["Australia" OR "Australian" OR "Australia's"] AND ["species" OR *divers* OR conserv* OR communit* OR assemblage* OR ecosystem* OR guild* OR tax*] NOT [*water* OR mari* OR aqua* OR sea OR ocean*] NOT ["New Zealand"]). In Google Scholar, a simpler keyword string was used instead ("Interim Biogeographic Regionali Australia"), retrieving the first 50 records. We constrained the date range to commence from 1995 (the year IBRA was first officially released; Thackway and Cresswell 1995) through to 2017. Duplicates were removed; and the reference lists of key biodiversity-focused studies using IBRA bioregions were cross-checked to ensure all relevant studies were captured.

To identify relevant studies, we implemented a stepwise screening process. This started with the application of a broad filter (based on a set of exclusion criteria), followed by use of a text mining technique (n-gram analysis) to prioritize a list of potentially relevant papers that was made available for a final, in-depth manual screening (O'Mara-Eves et al. 2015). A detailed description of the screening phase is provided in Online Resource 1. The 'Preferred Reporting Items for Systematic Reviews and Meta-Analysis' protocol (Moher et al. 2009) was followed, to record the results of our search and screening process (Fig. 1). EndNote X8.2 (Clarivate Analytics 2018) was used to manage references; and three packages in Program R program (R Core Team 2018)—`tm` (Feinerer et al. 2008), `RWeka` (Hornik et al. 2009) and `SnowballC` (Bouchet-Valat 2014)—were used to construct structured data from the text.

To characterize research on biodiversity for all relevant studies, we extracted a range of attributes, including: IBRA information (e.g., number of IBRA bioregions studied), spatial location, study design (e.g., type of analysis, data source, biodiversity response), focal entity (flora, fauna, and

ecosystem), and various biodiversity attributes (Online Resource 2). We also recorded information on the number of species and ecosystem services investigated. We used the shapefile of IBRA version 7 (Department of the Environment 2012) to spatially summarize the number of times bioregions and dimensions of biodiversity were reported. To represent this accurately, the four IBRA bioregions that lie outside of mainland Australia and Tasmania (i.e., Coral Sea, Indian Tropical Islands, Pacific Subtropical Islands, and Sub-Antarctic Islands) were omitted, and polygons extending across two or more administrative units were split based on state and territory boundaries, excluding Australia Capital and Jervis Bay territories due to their small scale and absence from relevant studies. This resulted in 32 bioregion polygons being artificially split into 71 discrete spatial units—hereafter referred as state-split discrete bioregions—and 53 bioregion polygons located exclusively within a state or territory—hereafter referred as full-extent discrete bioregions (Fig. 2).

In this systematic map, the development of evidence matrices was informed by the most salient themes covered in the biodiversity research literature (e.g., de los Ríos et al. 2018; Martín-López et al. 2009) and systematic analyses on the nature of scientific fields applied to biodiversity conservation (e.g., Cronin et al. 2014; Fardila et al. 2017). To provide an overview of the existing evidence on biodiversity research at the IBRA scale, we compared counts within and across all categories/groupings and calculated descriptive statistics for both the number of species investigated, and the number of times bioregions and dimensions of biodiversity were reported in relevant studies. We used ArcGIS 10.5.1 (ESRI 2017) to generate spatial data, and three R packages to analyze, summarize and visualize data: `dplyr` (Wickham et al. 2017), `ggplot2` (Wickham 2016) and `expss` (Demin 2018).

Quality assurance of evidence synthesis process

To minimize possible sources of bias and error, we started by structuring our overarching evidence-synthesis question to contain the population (P) and outcome (O) elements—often

referred as 'PO' question type (Collaboration for Environmental Evidence 2018; James et al. 2016). We used an iterative-keyword-screening process to identify the search strategy that best captured our studies of interest across three databases, and a stepwise process with pre-defined exclusion criteria to ensure our work is reproducible and transparent (Online Resource 1). The accuracy of the text-mining technique was estimated based on selective manual validation, and both the interpretation of our exclusion criteria and the reliability of the classification of relevant studies were independently examined (Online Resource 3). Due to the breadth of our topic, an explicit critical appraisal of study validity was impractical; this is justifiable given that it was unlikely to influence the collation, description and mapping process (Collaboration for Environmental Evidence 2018). We instead focused on removing duplicate publications of the same data to avoid double counting (Frampton et al. 2017), given that frequency of study attribute categories were pivotal to the reliability of our evidence synthesis.

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Results

Of the 15,190 references uncovered during the identification phase (Fig. 1), 67 studies met all eligibility criteria. The number of biodiversity-focused studies on IBRA bioregions published annually has increased over time (Online Resource 4), with more than half (58%) using bioregions based on the IBRA 6.1 revision, published in 2004 (Online Resource 5). The majority (65.7%) of relevant studies undertook biodiversity research inside only a single bioregion. For 18 of the studies, the reported bioregion was artificially split by administrative boundaries, with a fifth (19.4%) investigating biodiversity from bioregions extending across two or more administrative units. Five studies considered all bioregions found across the entire Australian continent (mainland and Tasmania), and in two studies, Tasmania was excluded.

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The frequency of relevant studies differed among bioregions, and within bioregion when its

area extends across two or more administrative units (Fig. 2). Nine of the 124 discrete spatial units into which IBRA bioregions were split were reported anywhere between 12 and 17 times (Online Resource 6). The largest number of times any of the 53 full-extent discrete bioregions (i.e., IBRAs found exclusively within one state or territory) was reported ranged from 6 to 17, in Tasmania and Queensland respectively (Table 1). Yet, in New South Wales and Victoria, a state-split discrete bioregion (i.e., IBRAs extending across administrative units) was more frequently reported than any full-extent bioregion found within their boundaries.

< Insert table 1 around here >

Nearly half (47.8%) of relevant studies were based exclusively on new data, but only two provided spatial information to locate sample sites (Table 2). Inferential analysis was used ~3.5 times more frequently than predictive or descriptive analyses (combined). Measures of species distribution and/or diversity were most common (68.7%), and 6/23 studies that considered biodiversity across multiple bioregions compared findings between bioregions (9% of all relevant studies).

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There were seven relevant studies that investigated biodiversity at the ecosystem level (Online Resource 7), all of which focused on one bioregion each or two bioregions ($n = 6$ and 1 papers, respectively). In six studies, the research topic was ecosystem functioning (Online Resource 8). The remaining study evaluated three provisioning and five regulatory ecosystem services provided by forests in the Wet Tropic bioregion, with this being the only bioregion reported twice.

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Of the 60 papers that investigated living organisms, species assemblages were used four and six times more frequently than species communities and single species, respectively (Online Resource 8). Fauna was the predominant and exclusive target across species studies (76.7%), and in only four studies, flora was investigated in combination with fauna. Out of the 55 species studies with enough information to classify species at higher taxonomic rank, 86 observations spread across 16 taxa were identified and examined. Mammals and birds were commonly studied, followed by reptiles and

vascular plants (Online Resource 9). Vertebrates, which constituted 67.4% of taxonomic records (Fig. 3a), were studied more frequently than plants (Fig. 3b) or invertebrates (Online Resource 10) in all discrete bioregions.

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Five of the 86 observations lacked enough information to identify how many species were studied at higher taxonomic rank, affecting four taxa (i.e., Aves, Arachnida, and Malacostraca only once, and Mammalia twice). Although the average number of species varied greatly between taxa—ranging from 1 to 692 species of non-vascular plants and insects, respectively—the standard deviation in the number of species that were studied was hundred or more for mammals, reptiles, snails/slugs, insects, and vascular plants (Online Resource 11).

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For the nine most-reported discrete bioregions (i.e., 12–17 relevant studies; Online Resource 6), similar frequency patterns are apparent for the categories of study design attributes (Table 3) and taxa (Fig. 4). The only striking difference is that research on biodiversity in the most-reported discrete bioregions was largely based on secondary data, and most of these considered biodiversity across multiple IBRA bioregions without comparing findings between bioregional spatial units (Table 3).

Discussion

Biogeographic classification schemes have been developed to prioritize conservation efforts, and have been repeatedly refined in some countries (e.g., IBRA is now up to its fourth official release [version 7]). However, the factors underpinning our understanding of biodiversity research within the context of such schemes has yet to be studied. Through a detailed look (evidence synthesis) at the scientific use of the IBRA framework, we found disparities in the relative effort given to different geographic, methodological and biodiversity foci, and a lack of integrative work spanning multiple bioregions.

Geographical bias

Research effort is distributed unevenly both among IBRA bioregions, and within bioregion when its area extends across two or more administrative units (Fig. 2). This suggests that Australia's state and territory boundaries are important determinants of the geographic extent of biodiversity research, taking priority over the integrity of IBRA bioregions as unit of analysis. Similar patterns have been observed, at a global scale, in efforts devoted to different countries, again likely driven by historical and political/administrative circumstances (Ahrends et al. 2011; Meyer et al. 2015). Although the planning units of the IBRA framework (i.e., bioregions) are independent from political boundaries, their demarcation and description were achieved by aggregating environmental information (e.g., Tasmania nature conservation regions, Queensland biogeographic regions) provided independently by states and territories (Thackway and Cresswell 1995). Further, the planning and management of natural resources in Queensland, for example, is driven by a hierarchical classification approach that merged the IBRA bioregions extending outside the state with those lying exclusively within (Wilson et al. 2002), which might have inadvertently promoted those bioregions as landscape features that are also, or can be confined to, political boundaries.

Methodological preferences

There are marked preferences on how biodiversity research within the context of the IBRA framework have been designed in the last two decades (Table 2). Unlike global trends, where a decline in fieldwork-based studies have been observed (Carmel et al. 2013; Ríos-Saldaña et al. 2018), we found that researchers largely used field data to carry out their analyses at a bioregional scale. This means that biases in biodiversity research may also stem from factors limiting the digitalization and access of first-hand collected data (Meyer et al. 2015). The large number of studies carried out at a relatively small scale (i.e., 65.7% of relevant studies undertook biodiversity research inside only a single IBRA bioregion) could amount to a considerable scientific output if their data were properly

stored in an open-access form (Hampton et al. 2013). This potential contribution is, however, hampered by the lack of geographic information on sample sites (e.g., 97% of relevant studies uncovered in this evidence synthesis), limiting accountability and replicability, and thus increasing the challenge in incorporating these data into national- or global-scale analyses.

The preference for pattern-based measures of biodiversity was expected, as these can be easily interpreted and readily used to investigate different spatial arrangements (alpha, beta and gamma diversity) of biodiversity (Colwell 2009) and are less sensitive to differences in survey design (Magurran et al. 2010). However, as a consequence of their community ecology focus, they provide less accurate estimates of autecological processes (e.g., population dynamics, species' dispersal), compared with more complex response measurements on individual species, or the directed study of species interactions (Fardila et al. 2017). We also found a higher proportion of inferential research compared to those that focused on the likelihood and magnitude of environmental changes or their underlying mechanisms (predictive and mechanistic approaches). Further, the lack of comparison between spatial units of analysis—IBRA bioregions in this review—is a limiting factor for systematic conservation planning (de los Ríos et al. 2018).

Biases in biodiversity foci

Our Australian findings reinforce the view that there is a bias towards species as the level of biological organization, as recorded in the global literature (Fazey et al. 2005; Velasco et al. 2015). As such, the emphasis on species occurrence and community/diversity metrics—60% of relevant studies investigating living organisms at IBRA scale conducted research at assemblage level—is at odds with the claim that species interactions and ecosystem processes enjoy a major emphasis in ecological research (Caliman et al. 2010; Nobis and Wohlgemuth 2004). However, research on single species is also rarely undertaken within the context of the IBRA framework, contrary to what has been found in other reviews (e.g., Fardila et al. 2017; Fazey et al. 2005). Further, our bioregion

findings align with previous literature reviews that have pointed out both the overrepresentation of mammals and birds (Clark and May 2002; Martín-López et al. 2009) and the lack of research on more speciose taxa (e.g., insects) or relatively highly threatened ones (e.g., amphibians), despite a slight increase in research effort towards poorly represented taxa in recent years (Di Marco et al. 2017).

The predominant focus of research on mammals and birds might also be linked to these taxa being perceived as umbrella or flagship species (de los Ríos et al. 2018; Hecnar 2009) which are conspicuous and more vulnerable to extinction in Australia (Johnson 2006; Loehle and Eschenbach 2012). Emphasis on highly visible and charismatic taxa is not new in the literature (Clark and May 2002; Ford et al. 2017; Martín-López et al. 2009). While such a focus can serve to attract public support to conservation, it also risks diverting conservation resources away from less alluring but nevertheless threatened species (Seddon et al. 2005) with important ecological roles (Gascon et al. 2015; Lavelle et al. 2006), whose protection might require less investment for a greater conservation impact (Walsh et al. 2013).

Implications for systematic conservation planning

The design of environmental policies has been linked to both knowledge on biodiversity and bioregionalized conservation schemes (Martín-López et al. 2009; Smith et al. 2018). As such, disparities in the relative effort given to where, what and how biodiversity has been investigated might undermine systematic conservation planning at large scales, due to assessments of biodiversity status, as well as past and future trends (and their drivers), being based on misleading baselines (Magurran et al. 2010; Mihoub et al. 2017). This could, in turn, translate into conservation policies, targets and actions (de los Ríos et al. 2018; Martín-López et al. 2009) that fail to achieve their intended goals (Di Marco et al. 2017; Pyšek et al. 2008). For example, incomplete knowledge on distributions and habitat use has been identified as a crucial factor influencing the listing of species as threatened and the development of plans for their recovery in Australia (Walsh et al. 2013).

To deal with biodiversity knowledge gaps, which limit our understanding of the relationship between biodiversity—ranging from genes to ecosystems—conservationists have proposed three main solutions: 1) greater effort directed towards poorly represented taxa in the scientific literature (Bonnet et al. 2002; Clark and May 2002); 2) development and maintenance of biodiversity databases, preferably open-source, relational in structure, and based on clear standards (Hampton et al. 2013); and 3) a more equitable allocation of funding for biodiversity research for meeting the above goals (Andelman et al. 2004; Clark and May 2002). Improvement has been reported for the first two points, as poorly represented taxa (e.g., insects) are increasingly salient as study organisms (Di Marco et al. 2017), and open-source, long-term databases continue to increase in number and quality (Ondei et al. 2018). Yet, biodiversity research largely depends on priorities set by funding organisms (Ahrends et al. 2011; Stroud et al. 2014). All this suggests that incomplete knowledge on biodiversity will be the norm for quite some time; therefore, conservationists and managers working at macroecological scales should consider the implications of, and account for gaps and biases in, research effort when designing policy instruments aimed to systematically conserve biodiversity. Our evidence synthesis is an important first step in that direction, as it provides an overview of where, what and how terrestrial biodiversity has been researched for almost a quarter of a century of systematic conservation planning at bioregional scale in Australia.

Compliance with ethical standards

Funding: This work was funded by Australian Research Council Laureate Fellowship (grant number FL160100101).

Conflict of interest All authors declare that they have no conflict of interest.

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FIGURE CAPTIONS

Fig. 1 Identification and selection of relevant studies used in our systematic mapping of biodiversity studies of Australian biogeographic units, based on application of the PRISMA protocol (Moher et al. 2009). Note: WoS, GS and IBRA respectively stand for Web of Science, Google Scholar and the Interim Biogeographic Regionalization for Australia

Fig. 2 Extent (expressed in percentage) of bioregions within administrative units (states and territories), and number of times discrete bioregions were reported in biodiversity studies. Note: IBRA stands for Interim Biogeographic Regionalization for Australia

Fig. 3. Number of times (a) vertebrates and (b) plants were investigated in discrete bioregions, based on relevant studies that had sufficient information to classify fauna and flora into higher taxonomic groups (n = 55). IBRA stands for Interim Biogeographic Regionalization for Australia

Fig 4. Number of times each taxon was represented in the most-reported discrete bioregions. Note: Most-reported refers to discrete bioregions that were reported ≥ 12 times. CYP, MAC, MUL, NAN, NET, NSS, PIL, RIV and WET respectively stand for: Cape York Peninsula, MacDonnell Ranges, Mulga Lands, Nandewar, New England Tablelands, New South Wales South Western Slopes, Pilbara, Riverina and Wet Tropics

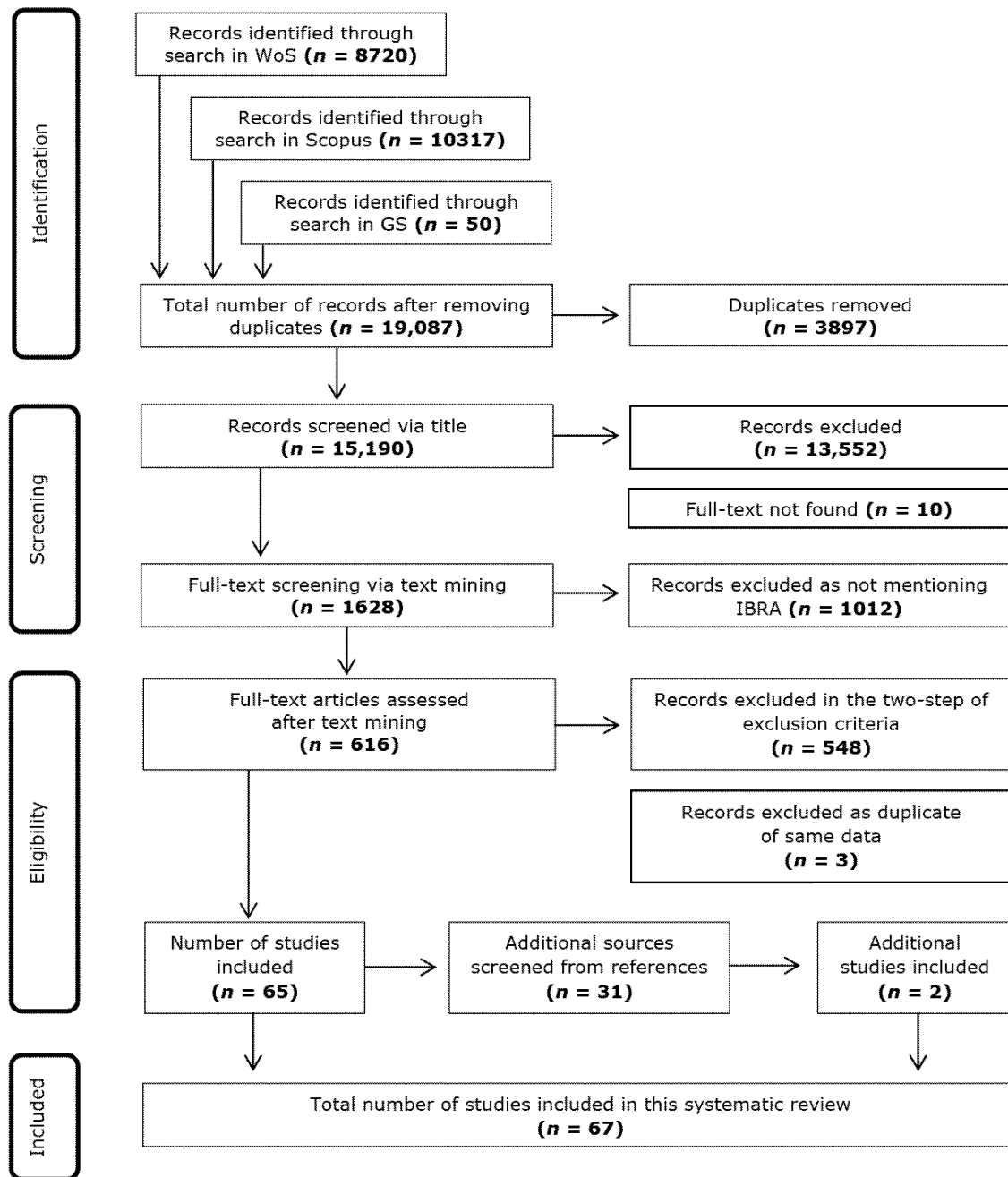


Fig. 1

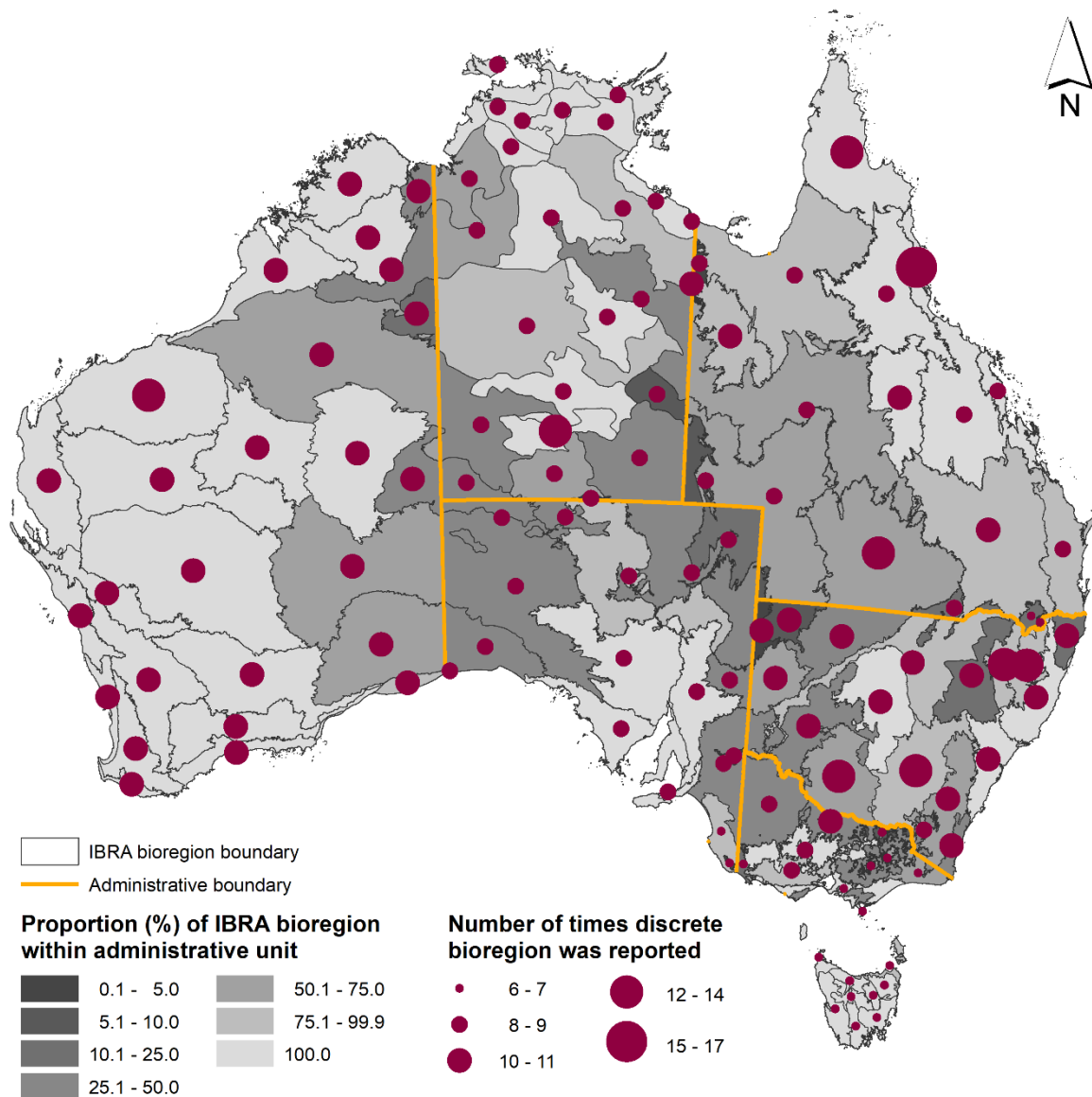


Fig. 2

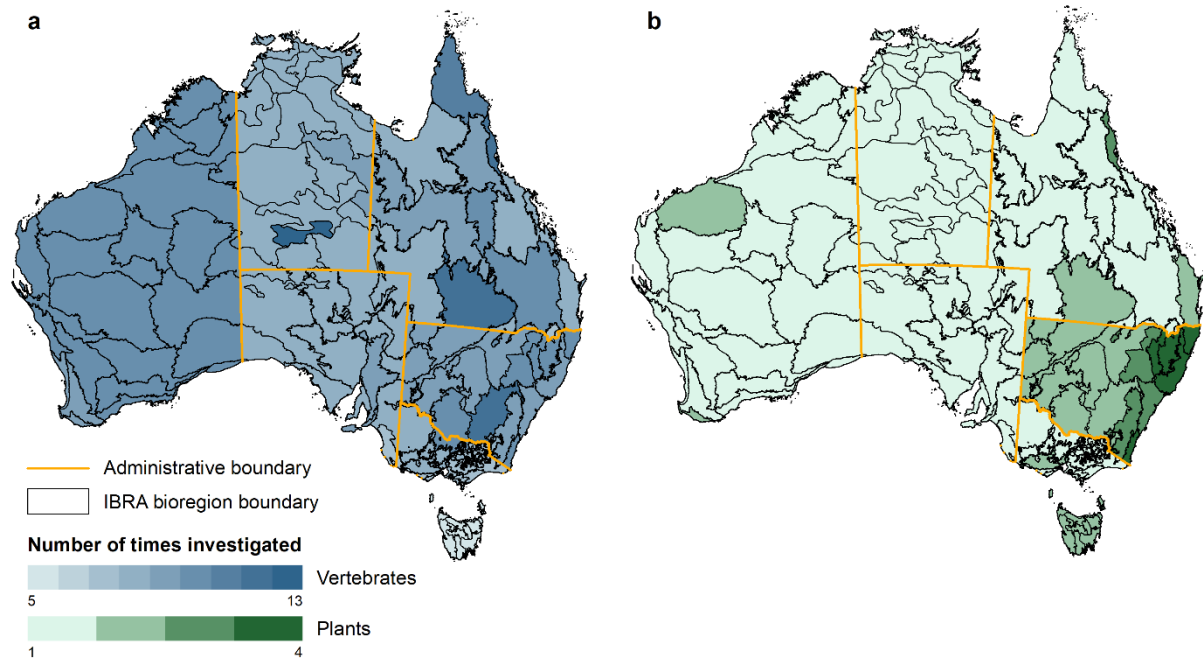


Fig. 3

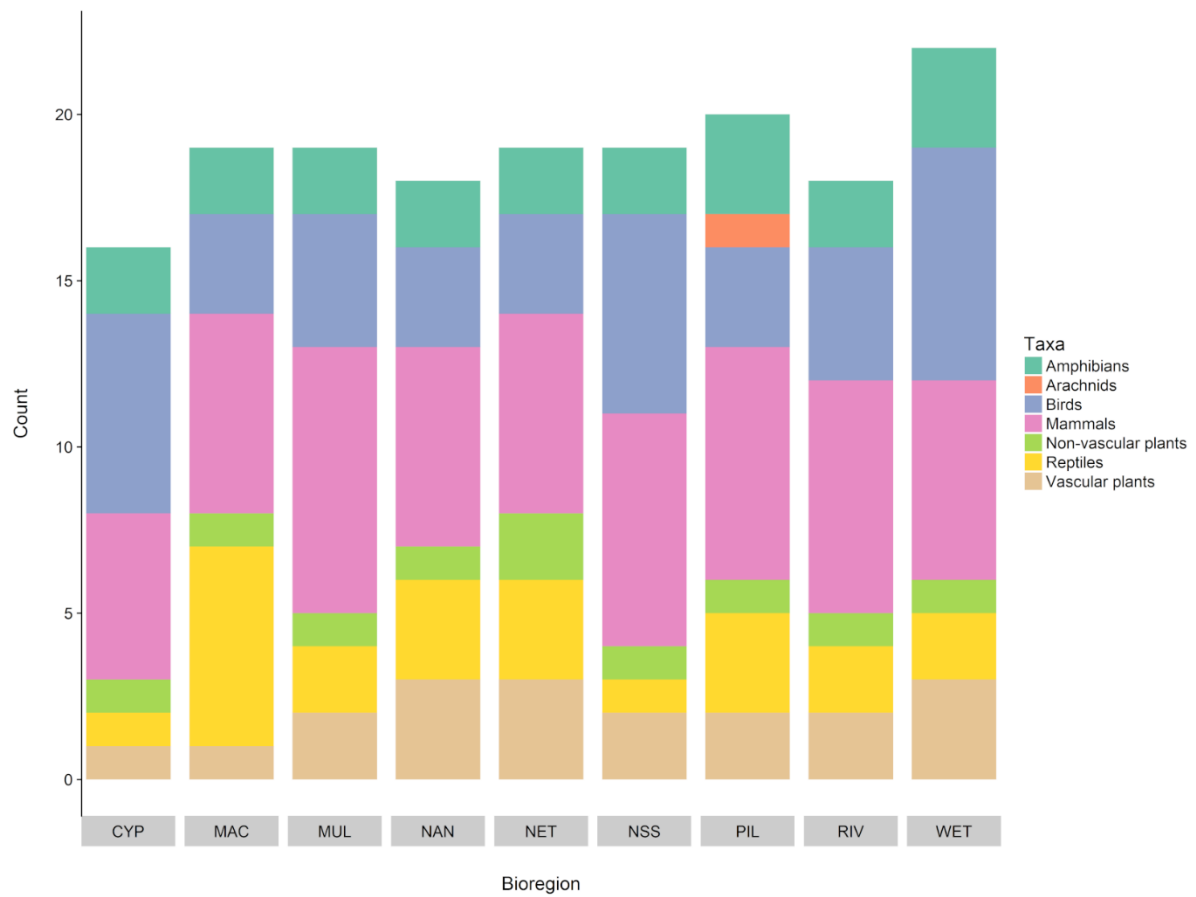


Fig. 4

TABLES

Table 1 Number of full-extent and state-split discrete bioregions within Australia's administrative units (n), and total, mean, standard deviation (SD), minimum (Min.) and maximum (Max.) number of times full-extent and state-split discrete bioregions were reported. Note: '-' = not applicable

Administrative Unit Type of discrete bioregion	With all relevant studies						
	n	Total	Mean	Median	SD	Min.	Max.
New South Wales							
Full-extent	3	31	10.3	10.0	0.6	10	11
State-split	15	162	10.8	10.0	1.26	9	14
Northern Territory							
Full-extent	12	101	8.4	8.0	1.4	8	13
State-split	13	107	8.2	8.0	0.6	8	10
Queensland							
Full-extent	6	65	10.8	10.0	3.4	8	17
State-split	12	106	8.9	8.0	2.0	7	14
South Australia							
Full-extent	4	34	8.5	8.5	0.6	8	9
State-split	13	102	7.9	8.0	0.4	7	8
Tasmania							
Full-extent	8	48	6.0	6.0	0.0	6	6
State-split	1	6	6.0	6.0	-	6	6
Victoria							
Full-extent	2	15	7.5	7.5	0.7	7	8
State-split	9	70	7.8	7.0	1.4	7	11
Western Australia							
Full-extent	18	185	10.3	10.0	0.6	10	12
State-split	8	80	10.0	10.0	0.0	10	10
Australia							
Full-extent	53	479	9.0	9.0	2.1	6	17
State-split	71	633	8.9	8.0	1.7	6	14

Table 2 Number of studies by categories of study design attributes (n), and mean, median, standard deviation (SD), minimum (Min.) and maximum (Max.) number of IBRA bioregions reported by categories of study design attributes. Note: '-' = not applicable. Description of categories for each attribute can be found in Online Resource 2

Attribute Categories	With all relevant studies					
	n	Mean	Median	SD	Min.	Max.
Data source						
Primary data	32	1.7	1.0	3.0	1	18
Secondary data	27	27.4	8.0	34.8	1	85
Primary and secondary data	8	1.6	1.5	0.7	1	3
Geographic analytical scope						
General	65	12.4	1.0	25.7	1	85
Localized	2	1.0	1.0	0.0	1	1
Type of analysis						
Inferential	50	9.7	1.0	22.4	1	85
Predictive	8	32.8	2.0	43.3	1	85
Descriptive	6	9.5	5.5	10.4	1	26
Mechanistic	3	1.3	1.0	0.6	1	2
Biodiversity response						
Distribution and/or diversity	46	12.6	1.0	26.4	1	85
Genetics	9	5.2	1.0	11.9	1	37
Population change	6	16.2	4.5	30.0	1	77
Species trait	3	26.7	2.0	43.6	1	77
Mechanistic relationship	3	1.3	1.0	0.6	1	2
Type of Study						
One bioregion	44	-	-	-	-	-
> 1 bioregion & no compare	17	43.3	26.0	35.4	2	85
> 1 bioregion & compare	6	4.3	2.5	3.3	2	9

Table 3 Administrative unit, extent of discrete bioregion within administrative unit (expressed in percentage), total number of times most-reported discrete bioregions were reported, and the percentage of times the categories for each of the study design attributes were used in most-reported discrete bioregions. Note: '-' = not applicable. Most-reported refers to those discrete bioregions that were reported twelve or more times. CYP, MAC, MUL, NAN, NET, NSS, PIL, RIV and WET respectively corresponds to Cape York Peninsula, MacDonnell Ranges, Mulga Lands, Nandewar, New England Tablelands, New South Wales South Western Slopes, Pilbara, Riverina, and Wet Tropics. NSW, NT, QLD, and WA respectively stand for New South Wales, Northern Territory, Queensland, and Western Australia. Description of categories for study design attributes can be found in Online Resource 2

Attribute Categories	Most-reported discrete bioregions								
	CYP	MAC	MUL	NAN	NET	NSS	PIL	RIV	WET
General information									
Administrative unit	QLD	NT	QLD	NSW	NSW	NSW	WA	NSW	QLD
Extent (%)	100	100	73.9	76.7	95.2	93.5	100	72.5	100
Times represented	12	13	14	12	12	14	12	12	17
Data source									
Primary data	16.7	15.4	21.4	25.0	16.7	35.7	16.7	8.3	29.4
Secondary data	66.6	84.6	71.5	75.0	83.3	57.2	83.3	83.4	53.0
Primary and secondary data	16.7	-	7.1	-	-	7.1	-	8.3	17.6
Geographic analytical scope									
Localized	-	7.7	-	-	-	-	-	-	-
General	100	92.3	100	100	100	100	100	100	100
Type of analysis									
Inferential	58.4	76.9	64.4	66.7	66.7	71.5	66.7	58.4	52.9
Predictive	33.3	23.1	21.4	25.0	25.0	21.4	25.0	25.0	47.1
Descriptive	-	-	7.1	8.3	8.3	7.1	8.3	8.3	-
Mechanistic	8.3	-	7.1	-	-	-	-	8.3	-
Biodiversity response									
Distribution and/or diversity	75.1	76.9	71.6	66.8	66.8	85.8	58.3	66.8	64.6
Genetics	-	7.7	7.1	8.3	8.3	-	25.0	8.3	5.9
Population change	8.3	7.7	7.1	16.6	16.6	7.1	8.3	8.3	17.6
Species trait	8.3	7.7	7.1	8.3	8.3	7.1	8.3	8.3	11.8
Mechanistic relationship	8.3	-	7.1	-	-	-	-	8.3	-
Type of study									
One bioregion	16.7	38.5	35.7	8.3	8.3	28.6	16.7	8.3	52.9
> 1 bioregion & no compare	66.6	61.5	64.3	83.4	83.4	64.3	83.3	83.4	41.2
> 1 bioregion & compare	16.7	-	-	8.3	8.3	7.1	-	8.3	5.9